

# Locations of Quantitative Trait Loci Conferring Russian Wheat Aphid Resistance in Barley Germplasm STARS-9301B

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## ABSTRACT

Russian wheat aphid (RWA, *Diuraphis noxia* Kurdjumov) infestations reduce grain yield and quality and have caused more than \$1 billion in losses for barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) in the western United States since 1986. Our objective was to map quantitative trait loci (QTLs) conferring resistance to RWA feeding damage in the germplasm line STARS-9301B via polymerase chain reaction-based marker assays of 191 F<sub>2</sub>-derived F<sub>3</sub> families from the cross 'Morex'/STARS-9301B. Morex is a susceptible six-rowed malting barley. STARS-9301B is a selection from RWA-resistant Afghanistan introduction PI366450. Replicated seedling reactions to RWA infestations were used to phenotype each family based on a 1 to 9 visual rating of chlorosis. A total of 107 molecular markers was used to construct a linkage map. Quantitative trait loci analysis identified two major QTLs for resistance. The QTL on the short arm of chromosome 1H was associated with B-hordein and explained 26% of the variation for RWA reaction. A QTL on chromosome 3H associated with EBmac0541 explained 38% of the variation. A minor QTL on chromosome 2H was associated with marker GBM1523 and explained 6% of the variation. A combined analysis indicated that the marker-QTL associations explained 59% of the phenotypic variation for RWA resistance. These markers linked with QTLs will be valuable in breeding for RWA resistance. Pyramiding the genes from STARS-9301B with genes from other sources will be helpful for long-term protection against RWA in barley.

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**Abbreviations:** I, intermediate; LRS, likelihood ratio statistic; PCR, polymerase chain reaction; QTL, quantitative trait locus; R, resistant; S, susceptible; SSR, simple sequence repeat; STS, sequence-tagged-site; TRAP, target region amplification polymorphism.

**R**USSIAN WHEAT APHID (RWA, *Diuraphis noxia* Kurdjumov) infestations have caused more than \$1 billion in losses to wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) in the western United States since they were first identified in Texas in 1986 (Morrison and Peairs 1998). Russian wheat aphid infestations reduce grain yield and quality of barley. Chemical control of RWA infestations is only accomplished by systemic insecticides, which are undesirable for environmental and economic reasons. Thus, research on RWA infestation and prevention through developing resistant cultivars is important. STARS-9301B and STARS-9577B were the first two RWA-resistant barley germplasm lines released (Mornhinweg et al., 1995b, 1999). Inheritance studies indicate different multiple gene control of resistance in these lines (Mornhinweg et al., 1995a, 2002). More recently, additional two-rowed and six-rowed RWA-resistant germplasm have been released (Mornhinweg et al., 2006b, 2007a,b), and the first resistant cultivars have been developed (Bregitzer et al., 2008; Mornhinweg and Porter, 2006) including 'Burton' (Bregitzer et al., 2005), which has resistance from STARS-9301B.

Published in Crop Sci. 48:1452–1458 (2008).

doi: 10.2135/cropsci2007.11.0651

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Prior genetic studies of STARS-9301B and STARS-9577B indicated that resistance was conferred by multiple genes in both lines and that the genetics of resistance was different between the two lines (Mornhinweg et al., 2002). STARS-9301B typically shows a highly resistant reaction to RWA feeding (2 on the 1–9 Webster's scale; Webster et al., 1991) and does not show the leaf chlorosis, leaf rolling, head trapping, and yield loss associated with susceptibility (Mornhinweg et al., 1995a, 2006a; Bregitzer et al., 2003). Genetic analysis suggested that RWA resistance in STARS-9301B was controlled by recessive epistasis of a dominant gene *Rdn2* on an incompletely dominant gene *Rdn1* (Mornhinweg et al., 1995a). The objective of this study was to determine the location of quantitative trait loci (QTLs) conferring RWA resistance in STARS-9301B.

## MATERIALS AND METHODS

### Plant Materials

A mapping population was developed using the susceptible malting barley cultivar Morex (Rasmusson and Wilcoxson, 1979) with STARS-9301B. STARS-9301B is a RWA-resistant six-rowed spring barley (Mornhinweg et al., 1995b) selected from PI366450, an accession collected in Afghanistan. The  $F_1$  plants were grown to produce  $F_2$  progeny that were used to produce a population of  $F_{2:3}$  families. A random set of 191  $F_{2:3}$  families was used for mapping.

### Russian Wheat Aphid Infestation

Russian wheat aphid infestation scores for  $F_2$  plants were derived by averaging RWA infestation scores on  $F_3$  progeny to get an infestation score unbiased by variation in environment and aphid feeding behavior. For each  $F_2$  plant, 30  $F_3$  progeny were sown in rows in flats in an augmented block design (Federer, 1993) in the greenhouse. Flat layout, check rows, and infestation were as described in Mornhinweg et al. (1995a). Seedlings were rated for RWA infection after 3 wk of infestation and classified as resistant (R), intermediate (I), or susceptible (S) using the 1 to 9 scale developed by Webster et al. (1991) as described (Mornhinweg et al., 1995a, 2002): 1 to 3 for resistant plants, 4 to 6 for intermediate plants, and 7 to 9 for susceptible plants. Infestation experiments were conducted twice. The phenotypic value of each  $F_2$  family was calculated by averaging the LS means (adjusted based on the nearest check rows) of the  $F_3$  progeny in SAS (SAS Institute, Cary, NC).

### Marker Screening

From each of the 191  $F_{2:3}$  families, 10 seeds were planted. Leaf tissue was harvested from 6- to 8-wk-old seedlings. Plants from each family were pooled for DNA extraction (Dellaporta et al., 1983) and quantification.

Morex and STARS-9301B were screened for polymorphism using simple sequence repeat (SSR) markers (Ramsay et al., 2000; Varshney et al., 2007; Beaubien and Smith, 2006), target region amplification polymorphism (TRAP) markers (Hu and Vick, 2003) and a B-hordein marker amplified by primers KV1/KV2 (Kanazin et al., 1993). The SSR markers were amplified in 20- $\mu$ L reactions as described by Dahleen et

al. (2003). The  $MgCl_2$  concentrations and template concentrations were modified for some SSR markers for better amplification. The SSR products and the B-hordein marker were separated on polyacrylamide gels (Wang et al., 2003). The TRAP markers were tested using fixed primers for resistance gene analog NLR for and RLK rev (Chen et al., 1998) and telomeric sequences TeloRT and TeloRG, and arbitrary primers sa12-700 and ga3-800 (Hu, 2006).

### Mapping and QTL Analysis

Markers polymorphic between Morex and STARS-9301B were tested on the  $F_{2:3}$  families and scored as homozygous Morex, homozygous STARS-9301B, or heterozygous. Genetic linkage maps were constructed from the data using the computer program Mapmaker, version 2.0 for Macintosh (Lander et al., 1987; Lincoln et al., 1992). Data-type  $F_2$  intercross was used for constructing maps. Linkage groups were assembled using the *GROUP* command at LOD 5.0. The markers that did not fit in the groups were assigned to the groups one at a time using the *TRY* command to choose the best position while keeping close to the published marker order. The robustness of the marker order in a linkage group was checked using the *RIPPLE* command. The *MAP* command was used to determine linkage distances with the Kosambi map function (Kosambi, 1944).

Quantitative trait loci analyses for RWA resistance were conducted using marker regression and interval mapping in the software program Map Manager QTX (Manly et al., 2001). The probability value of false positive linkage  $P = 0.0001$  was chosen to provide evidence of linkage because "linkage at  $P = .05$  and  $P = .01$  is considered to be suggestive only" (Chmielewicz and Manly, 2002). Threshold genomewide values for QTL detection were determined by 5000 permutation tests (Churchill and Doerge, 1994). Composite interval mapping was conducted to reduce the effects of background QTLs, where multiple putative QTLs for RWA resistance seem to appear in the same region, adding the marker with greatest coefficient of variation to the background in the regression analysis (Chmielewicz and Manly, 2002). The *Evaluate interval QTL only* option was selected so that the likelihood ratio statistic (LRS) would test the incremental effect of the next QTL. The interaction test was performed to look for interactions or epistatic effects between the markers associated with resistance to RWA. Data Desk v4.1 (Data Description, Inc., Ithaca, NY) was used to determine the total phenotypic variation explained by the QTLs by performing multiple regression analysis. Also the interaction results from Map Manager QTX were confirmed using this program. The 95% confidence interval for individual QTLs was established by bootstrapping (Darvasi and Soller, 1997). The critical LRS threshold level was determined by 1000 permutation tests.

Associations between marker and phenotypic data for the families were determined using ANOVA (SAS Institute, Cary, NC) at  $P < 0.001$ . Markers were tested for segregation distortion by Chi square analysis with a 1:2:1 expected ratio.

## RESULTS

Russian wheat aphid phenotypic data showed significant differences among the  $F_{2:3}$  families, and infestation scores

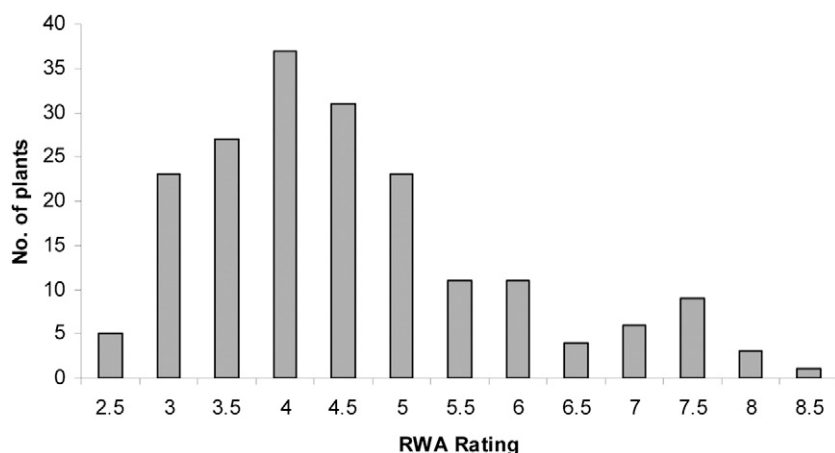


Figure 1. Distribution of mean Russian wheat aphid (RWA) ratings in 191  $F_{2:3}$  families from 'Morex'/STARS-9301B. Each adjusted LS mean represents the rating of two experiments with 30 plants tested per family in each experiment. Morex RWA rating = 7.4; STARS-9301B RWA rating = 2.2.

ranged from 2.5 to 8.3. STARS-9301B was rated at 2.2, while Morex was rated at 7.4. The distribution of the families was skewed toward the resistant parent, with an overall family rating of 4.6 (Fig. 1).

Polymorphisms were identified for 123 of the 432 tested SSR markers and the B-hordein marker KV1/KV2, and 29 polymorphic bands were identified by TRAP. A total of 107 markers was used to construct the linkage maps (Fig. 2). The remaining markers were omitted because they were unlinked or formed separate linkage groups at an LOD of 5.0. The order of markers was consistent with previously published maps (Varshney et al., 2007; Ramsay et al., 2000; Liu et al., 1996) except for marker GBM1480 on chromosome 1H, which has been mapped to the centromere region on the barley consensus map (Varshney et al., 2007) but was located proximal to the centromere on the long arm in our map. There were some differences in marker distances compared to the consensus maps, as expected with a different mapping population. Marker distribution was relatively even on chromosomes 2H and 4H, but gaps of 30 to 40 cM were observed on other chromosomes due to lack of polymorphism (Fig. 2). Chromosomes 1H and 3H each had one marker gap greater than 30 cM, while chromosome 5H had three and 7H had two gaps larger than 30 cM. The long arm of chromosome 6H was not covered with markers because of a paucity of SSR markers in the region (Ramsay et al., 2000). The total map distance was 1308.8 cM in Morex/STARS-9301B, with an average distance of 12.2 cM between markers.

Simple interval mapping and composite interval mapping revealed two highly significant QTLs for STARS-9301B associated with RWA resistance ( $P < 0.0001$ ). The short arm of chromosome 1H harbored the first QTL (Fig. 3; Table 1), QRdn2-1H-1. The QTL explained 26% of the phenotypic variation associated with RWA reaction. The QTL was significant with an LRS of 83.8 ( $P$

$< 0.0001$ ) associated with B-hordein. The 95% confidence interval for the QTL was 12 cM; that is, the QTL was located within 12 cM distance in the interval estimated by bootstrapping. The second QTL, QRdn1-3H-16, was located on the long arm of chromosome 3H associated with EBmac0541 (Fig. 3; Table 1), significant at an LRS of 91.6 ( $P < 0.0001$ ). It explained 38% of the phenotypic variation for RWA resistance. The confidence interval developed by bootstrapping was 7 cM. Multiple regression analysis estimated the total phenotypic variation explained by the chromosome 1H and 3H QTL as 54.5%.

In marker regression analysis, markers B-hordein and EBmac0541 were hidden by adding the markers to the background to identify additional markers significantly associ-

ated with the RWA resistance trait. No other marker on chromosomes 1H or 3H was significantly associated with the RWA resistance. Although there were extra peaks on chromosome 1H, composite interval mapping determined that these peaks were false or not significant.

Marker regression showed that GBM1523 on chromosome 2H was significantly associated with the RWA resistance trait at an LRS of 25.6 ( $P < 0.001$ ). A QTL QRdn3-2H-3 was detected from composite interval mapping explaining 6% of the phenotypic variation for RWA resistance. Other peaks were not significantly associated with RWA-resistance trait. The confidence interval was 49 cM, indicating that precise placement of this potential QTL was problematic. Adding GBM1523 to the multiple regression analysis increased the total phenotypic variation explained by the three QTLs to 59.4%. The interactions between the markers associated with the QTLs were not significant in multiple regression models, indicating there was no epistasis.

## DISCUSSION

In this study, we identified two highly significant QTLs in STARS-9301B, one on the short arm of chromosome 1H and other on the long arm of chromosome 3H, that explained 26% and 38% of the phenotypic variation, respectively. A third significant QTL explaining 6% of the phenotypic variation was located on chromosome 2H. The QTL detected on chromosome 1H was determined to be within a 12-cM confidence interval. Marker B-hordein is in a region of medium recombination ( $1\text{--}4.4\text{ Mb cM}^{-1}$ ; Kunzel et al., 2000). Therefore, the confidence interval for the QTL on chromosome 1H should cover approximately 12 to 52.8 Mbp. The confidence interval for the QTL on 3H is 7 cM and is in an area of high recombination ( $<1\text{ Mb cM}^{-1}$ ), which represents approximately 7 Mbp. The confidence interval is inversely proportional



to the strength of the QTL and the square of the number of the progeny. It is little affected by the spacing of marker loci, and even with a strong QTL and large sample population, the confidence interval is unlikely to be less than 10 cM (Chmielewicz and Manly, 2002). Hence, this study was robust in detecting the two major QTLs.

$F_{2.3}$  families were used for QTL identification instead of a more advanced generation because of the complex interactions proposed for STARS-9301B. Inheritance studies indicated two genes, one incompletely dominant and one dominant with epistatic effects, controlled RWA resistance in STARS-9301B (Mornhinweg et al., 1995a). Using the average phenotypic values of  $F_3$  progeny derived from selfing an  $F_2$  is more powerful than an  $F_2$  design (Zhang and Xu, 2004); thus, using this type of design increases the power of QTL detection. Unlike the initial genetic studies on STARS-9301B, we found no evidence for epistasis in our QTL analysis. The original genetic analysis (Mornhinweg et al., 1995a) showed the RWA reaction of  $F_{2.3}$  families fit a two-gene model, and segregation in backcross progeny provided evidence for epistasis based on the fit to a 3R:6I (rating of 3):3I (rating of 4):4S genetic ratio. Our analysis identified two QTLs with large effects on chromosomes 1H and 3H but also showed a third QTL on chromosome 2H. The presence of this third QTL could be responsible for the original hypothesis of epistasis among the genes for RWA resistance.

Previously, molecular markers associated with RWA resistance were identified in the barley lines PI366444 and PI366453 (Nieto-Lopez and Blake, 1994). These accessions were collected from Afghanistan at the same time as PI366450, the parent of STARS-9301B. They found two regions in the barley genome associated with RWA resistance. In both lines, the resistance for RWA was associated with the sequence-tagged-site (STS) PCR markers B hordein and D14 on the short arm of chromosome 1H. We found a QTL in the same region in STARS-9301B associated with the B-hordein marker. Nieto-Lopez and Blake

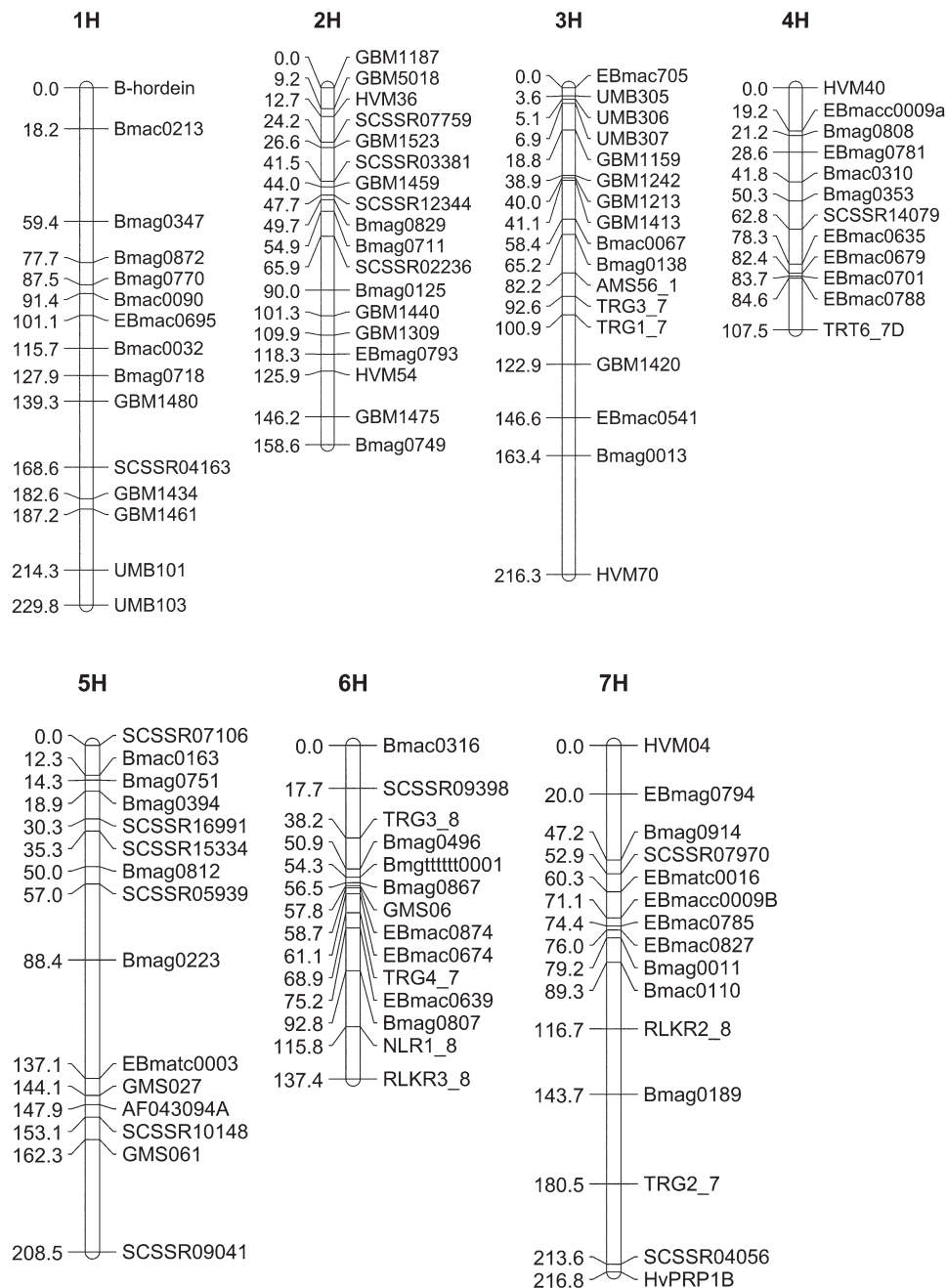


Figure 2. Genetic linkage maps of the seven barley chromosomes. Marker names are on the right side of each chromosome and cumulative linkage distance (in centimorgans) is on the left.

**Table 1. Locations and statistics for the Russian wheat aphid resistance quantitative trait loci (QTLs) in STARS-9301B. The QTLs were named after the conventional nomenclature: resistant (R) to *Diuraphis noxia* followed by chromosome name and BIN number.**

QTL	Associated marker <sup>†</sup>	95% CI <sup>‡</sup>	LRS <sup>‡</sup>	R <sup>2</sup> <sup>‡</sup>
		cM		
QRdn2-1H-1	B-hordein	12	83.8	26
QRdn1-3H-16	EBmac0541	7	91.6	38
QRdn3-2H-3	GBM1523	49	25.6	6
Total variation				59.4

<sup>†</sup>Markers significantly associated with the QTL in marker regression,  $P < 0.001$ .

<sup>‡</sup>95% CI, the interval span of the QTL; LRS, the likelihood ratio statistic at which the QTL is significant;  $R^2$ , the phenotypic variation explained by the QTL.

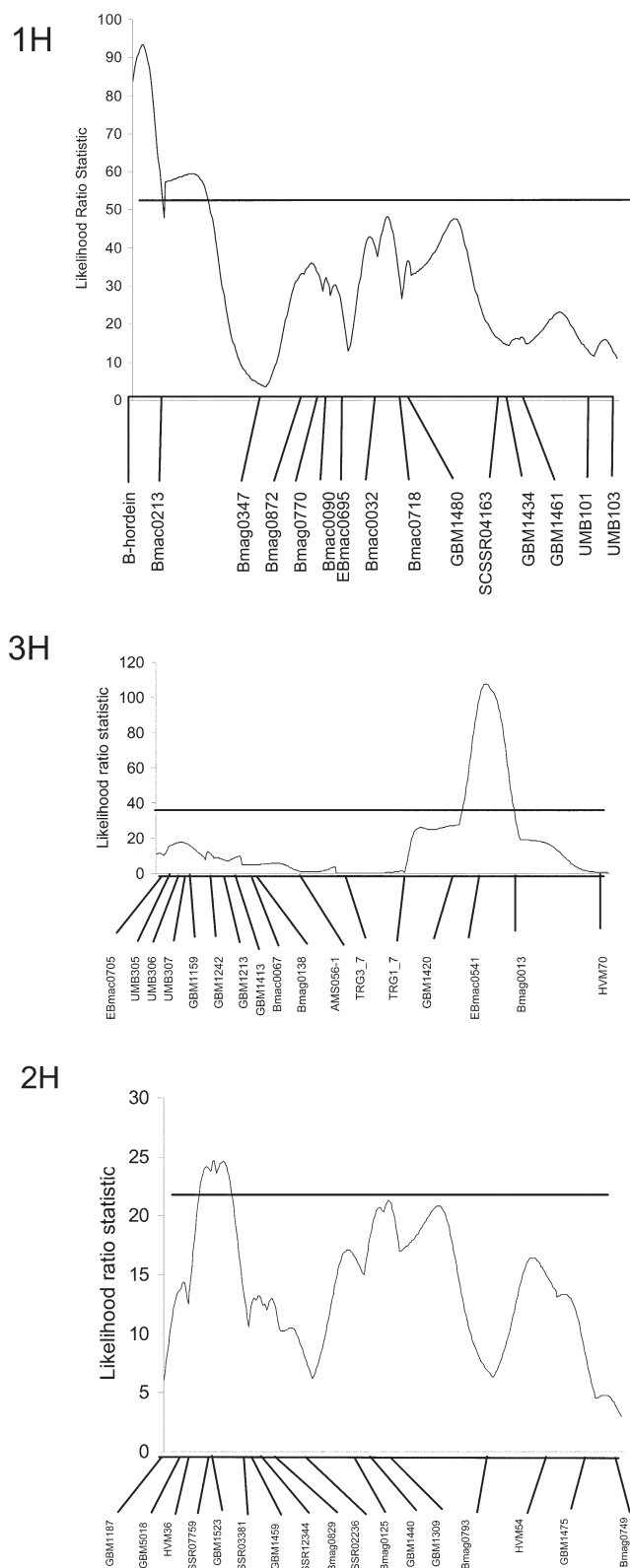


Figure 3. Chromosome maps and likelihood ratio statistics (LRS) for chromosomes 1H, 3H, and 2H. Marker designations and relative positions are at the bottom. The LRS graph shows the strength of association between markers and Russian wheat aphid (RWA) resistance. Markers B-hordein (1H), EBmac0541 (3H), and GBM1523 (2H) were significantly associated with RWA reaction ( $P < 0.0001$ ). The horizontal line for each graph indicates the LRS threshold for significance.

(1994) found that leaf rolling caused by RWA was associated with STS PCR marker ABG8 in Bin 3 on the short arm of chromosome 2H in one cross, near the minor QTL we found in STARS-9301B. It is likely that the chromosome 1H and 2H regions identified by Nieto-Lopez and Blake (1994) are allelic to QRdn2-1H-1 and QRdn3-2H-3 we identified in STARS-9301B. They did not find any associations between RWA resistance and markers on chromosome 3H, indicating that PI366444 and PI366453 do not contain QRdn1-3H-16.

Examining synteny between barley and wheat, there are as many as 10 genes for resistance to RWA in wheat. The genes *Dn1*, *Dn2*, *Dn4*, *Dn6*, *Dn8*, and *Dnx* are all located on the short arm of wheat chromosome 7D, and some of these genes may be allelic (summarized by Liu et al., 2001, 2005). *Dn5* was located on the long arm of chromosome 7D (Heyns et al., 2006). The *Dn7* gene is located in the 1RS segment of the 1RS/1BL translocation and is the only named gene providing wheat resistance to RWA biotype 2 (Lapitan et al., 2007). *Dn4* (Ma et al., 1998) and *Dn9* (Liu et al., 2000) were mapped to the short arm of wheat chromosome 1D, which is homeologous to barley chromosome 1H. None of the wheat genes were located on the group 2 or 3 chromosomes.

Many wheat lines with resistance to biotype RWA1 are susceptible to biotype RWA2, but barley lines such as STARS-9301B and other resistance sources show resistance to both RWA1 and RWA2 biotypes (Mornhinweg et al., 2006a). The QTL on chromosome 1H shows dominance with RWA scores for the homozygous resistant lines averaging 4.1, heterozygous lines 4.2, and homozygous susceptible 5.9. This QTL is likely the gene *Rdn2* for resistance to *Diuraphis noxia* (Mornhinweg et al., 2002). The QTL on chromosome 3H shows additive effects with RWA scores for the homozygous resistant lines averaging 3.6, heterozygous lines 4.2, and homozygous susceptible 5.8. This QTL is likely *Rdn1* (Mornhinweg et al., 2002).

This study has revealed the positions of two major QTLs on chromosomes 1H and 3H and suggested the presence of an additional QTL for RWA resistance on chromosome 2H. Fine QTL mapping projects can use this information for saturating these regions with more markers, thereby saving time, effort, and funds. The recent identification of five new biotypes of RWA on wheat in the United States (Haley et al., 2004; Burd et al., 2006) indicates the potential danger of emergence of new biotypes in future. Gene pyramiding would be useful to introduce genes for resistance to multiple biotypes of RWA as and when new sources of resistance are identified in a range of environments. Combining RWA resistance genes may decrease the problem of RWA overcoming resistance since the pest would need to deal with each resistance gene. Mapping additional genes for RWA resistance may help to achieve these objectives.

## Acknowledgments

This research was supported in part by the USDA/CSREES Regional Barley Genome Mapping Project. The authors thank Jinguo Hu and Angelia Hogness for help with TRAP markers and Nancy Hillen and Molly Taffe for laboratory assistance.

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